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ON THE CLASSIFICATION OF CERTAIN GROUPS OF BIRDS.

(SUPERSUBORDERS : ARCHORNITHIFORMES ; DROMÆOGNATHÆ ;
ODONTOHOLCÆ.)

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INTRODUCTION.

FOR a number of years I have paid considerable attention to the anatomy of birds, and especially to the osteology of the class. This has been done chiefly with the view of enabling me sometime to draw up a provisional scheme of classification of this group of the Vertebrata. This is now well on its way toward completion, but before finishing it I prefer to await the appearance of other taxonomical schemes by other authors, either now in press or coming out in parts, as well as the publication of certain memoirs of my own on the same subject. My work on the osteology of birds came to assume such formidable proportions that I failed to find a publisher either in this country or Europe who would undertake the publication of it. Therefore I was compelled to issue it in the form of separate memoirs, or monographs, many of which have already appeared, while eight others have been accepted and will be issued in due course.

In the present contribution I offer the researches I have made in the osteology of the Archæopteridæ, the Ornithuræ, or ostrich forms, and the Odontoholcæ. In doing this I have gone most carefully over all the literature on the subject that was available to me, and have examined a number of the skeletons of the birds contained in these groups, by far the larger share of which belonged to the department of comparative anatomy of the United States National Museum, to which institution I am especially indebted for the facilities it extended

to me. My thanks are particularly due to Mr. Lucas for his many courtesies in bringing the material before me, and to the free use of the collections under his charge. I am also indebted to my friend the late Prof. E. D. Cope, the late Prof. O. C. Marsh, and others for suggestions.

With these brief prefatory remarks given by way of explanation we may next proceed to the consideration of Order I of the class Aves, — the Saururæ, and the other groups enumerated above.

I. ORDER SAURURÆ.

SUPERSUBORDER.	SUBORDER.	SUPERFAMILY.	FAMILY.
Archornithiformes.	Archornithes.		Archæopterydæ.

So widely known is the fossil material representing the celebrated species of *Archæopteryx* that any very extended description of it would be quite unnecessary in this place. A great deal has been written upon the two species of this extinct genus since 1861, when Hermann von Meyer described the first specimen, which was probably nothing more than the impression of a primary feather discovered in the lithographic slate of Solenhofen, in Bavaria, a deposit belonging to the Upper Jurassic.

Two years afterward Owen described the first skeletal remains found in the same locality, it being largely the posterior part of the bird now known to science as *Archæopteryx lithographica*. A far more perfect example was found in 1877, from which the skull and the greater part of the skeleton could be made out. The first of these specimens is now in the British Museum, and the last one in the Museum of Berlin. It has never been the fortune of the present writer to have personally examined any of this material. In addition to the literature of the subject, however, I have before me a fine photograph of the British Museum specimen, which was secured by the Century Company of New York City to illustrate an article of mine in the *Century Magazine* (January, 1886). The majority of those illustrations were reproductions of my own drawings and among them a restoration I had made of *Archæopteryx*, but had I this restoration to make again, it would present a very different appearance, especially in the covering of the

body and the characters of the long tail. It favors its reptiloid organization too much, for it is probable that the typical species of the genus *Archæopteryx* were about seventy-five per cent bird and but twenty-five per cent reptile. If the fossil remains of the earlier ancestral stock of this group of forms are ever discovered we will meet with types presenting just as much of the reptile in their organization as bird, but they will not have developed the feathers that *Archæopteryx* possessed, nor will the hind limbs be as ornithic in structure. Some of these long-tailed reptiloid birds were about the size of a fish crow, while others were much larger. As is well known, they had a long, lizard-like tail composed of twenty-one vertebræ, and into the skin that covered these were inserted twenty-one pairs of conspicuously developed tail feathers, a pair to each vertebra. Morphologically, these long and slender joints were distinctly reptile in character, and doubtless had quite as much motion, individually and collectively, as do the vertebræ in any of our larger whip-tailed lizards of the present time. The comparatively small, pyramidal skull of these ancient forms was much flattened above, with its occipital aspect truncated obliquely. Either orbital cavity was large, and true teeth in grooves, or sockets, armed either mandible.

Reptilian characters largely predominated in the remainder of the vertebral column of *Archæopteryx*, for the articular surfaces of such of the vertebræ as have thus far been examined and studied are flat, and the sacral ones were few in number.

According to Marsh the sternum was represented by a single broad plate of bone, and it is likely that it developed a keel. The shoulder girdle was very birdlike, especially the *os furcula*. Pycraft, who has examined all the fossil specimens of these Jurassic birds, says: "The dorsal ribs have been described as wanting uncinatè processes; an unsafe conclusion, since these are often absent in the skeletons of existing birds, having been lost in maceration. The cervical ribs appear to have been much more slender than in modern birds, and to have remained movably articulated throughout life. 'Abdominal ribs,' resembling rather those of the *Crocodylia* than of the *Chameleonida*, appear to have been present."

The three bones composing one-half of the pelvis were apparently distinct, quite as much so as among the young of modern birds. Of these pelvic bones the ilium is best seen, and is said to be characteristically avian. Apart from a few transitional characters denoting the origin of the form from reptilian stock, the skeleton of the pectoral and pelvic limbs are almost entirely ornithic. Whether the avian-like humerus was pneumatic has not as yet been definitely decided. This is due to the fact that the pneumatic fossa is still concealed in the matrix. A low pectoral crest was developed, a feature we would naturally look for, as doubtless these birds could fly well. Three well-developed digits composed the skeleton of either hand; the first, or pollex, having two phalanges, index three, and medius four. All of the distal or ungual phalanges supported claws. The carpus, according to Pycraft, "probably agreed with that of modern birds; except that the distal mass of fused bones remained distinct throughout life, and that digit III was provided with a separate carpal bone." Every anatomist who has examined the pelvic limbs of these fossil forms declares that the skeleton of the pelvic limb is almost entirely avian in character, Professor Gadow having noticed that the metatarsal to the hallux digit was short and free, being directed backwards. Others have observed, as Professor Dames and Dr. Hurst, the reduction of the distal extremity of the fibula, but whether the bone stands in front of the tibia, as in *Iguanodon*, and stated by Dr. Stejneger, seems to be doubtful. The metatarsals were elongated as in existing birds, and apparently firmly ankylosed together, though their original separateness is easily made out by the presence of the sutural lines between their shafts. Including the hallux there were four toes, as in the higher bird groups of this day, and their ungual phalanges were all armed with a horny claw. *Archæopteryx* possessed a femur departing in general structure and appearance but very little from what characterizes that bone in any medium-sized corvine type of the present time, and so requires no special description. There seemed to be, however, considerable curvature to its shaft. In addition to the authorities I have already named as having contributed to the knowledge of these Jurassic birds, may be added

the names of Huxley, Dollo, Fürbringer, Romanes, Seeley, Woodward, and Zittel. Each and all of these writers have taught that, by extremely slow and gradual development in time, our existing birds were derived from ancestral reptilian forms, and that the discovery of such a genus as *Archæopteryx* need create no surprise, for it represents just such a type as we would look for far back in geologic time during the earlier transitional stages in the evolution of the class Aves.

The American Jurassic has also furnished fossil remains of another land bird, but whether arboreal or not, as was the case with *A. lithographica*, cannot be determined from the limited material. It was a toothed bird of some considerable size, and was described as *Laopteryx priscus* by Marsh, who obtained it from the Jurassic of Wyoming. It is principally represented by the posterior portion of a skull, and this, it is said, presents a somewhat struthious character. The single tooth found near this skull was more or less like the teeth possessed by *Ichthyornis*.

Beyond the fact, however, that *Laopteryx* probably belonged to the same geological age as did *Archæopteryx*, there is nothing to indicate in the remains we have what manner of appearing bird it was, much less as to whether it possessed a tail like *Archæopteryx*. It is provisionally placed here in the order Saururæ for convenience only.

II. ORDER ORNITHURÆ.

SUPERSUBORDER.	SUBORDER.	SUPERFAMILY.	FAMILY.
Dromæognathæ.	Struthionithes.		Struthionidæ.
	Rheornithes.		Rheidæ.
	Casuariornithes.		{ Dromaiidæ.
			{ Casuariidæ.
			{ Dromornithidæ.
	Dinornithes.		Dinornithidæ.
	Æpyornithes.		Æpyornithidæ.

Fürbringer employed the term Ornithuræ to designate his Subclass II of birds, created to contain all existing and extinct species of this group of vertebrates not included in Subclass I, the Saururæ, which is represented alone by the fossil *Archæopteryx*

lithographica and its allies. Gill, Stejneger, and others have used the term *Eurhipiduræ* for all birds in contradistinction to the *Saururæ*, while the last-named author throws the toothed birds of the American Middle Cretaceous outside of it. Now as *Eurhipiduræ* means "fan-tailed birds," it is a term not strictly applicable, for neither the struthious birds nor the grebes possess fan tails, while it is more than likely that the representatives of the ichthyonine birds did, and this very probably was the case too with *Hesperornis*. As with so much that now goes in avian taxonomy, even the lizard-tailed (*Saururæ*) and the bird-tailed (*Ornithuræ*) orders can only be considered provisional divisions. However, they can do duty until the day comes when a fossil bird is discovered somewhat more reptile-like than *Ichthyornis*, but presenting in the skeleton of its tail a decided advance birdwards from *Archæopteryx*, even to the point of the first stages of the formation of a pygostyle.

SUPERSUBORDER DROMÆOGNATHÆ.

In this group it is intended to include all the existing and extinct struthionine birds which are morphologically closely allied to the ostrich (*Struthio camelus*). This will include the *Dinornithidæ*, but obviously exclude the *Apterygidæ*, the *Crypturidæ*, and other families that are not ostriches in any sense of the word, any more than was the American cretaceous toothed loon, the *Hesperornis*. It comes about as near the expression of true avian affinities to associate the tinamous with the ostriches, for the reason that the posterior extremities of their ilia and ischia have remained free, as it would be to relegate the cassowaries to the crane group, simply because in them those bones fuse together in the adult.

The supersuborder *Dromæognathæ* includes the following suborders, namely: (1) *Struthiornithes*; (2) *Rheornithes*; (3) *Casuariornithes*; (4) *Dinornithes*; (5) *Æpyornithes*.

Of these the *Struthiornithes* are represented by the existing African ostriches of the family *Struthionidæ*. The *Rheornithes* include the South American ostriches of the family *Rheidæ*, of which there appear to be at least three well-defined species.

The Casuariornithes include three well-marked families, — the Dromaiidæ, the Casuariidæ, and the Dromornithidæ. The Dromaiidæ contain the emeus, the ostrich birds of Australia, of which there are two species, *Dromæus novæ-hollandiæ*, and *D. irroratus*.

The second family of the Casuariornithes or the Casuariidæ includes the cassowaries, other ostrich birds of the Australian region, of which there are at least nine existing species of the genus *Casuarius*. The cassowary of the island of Ceram is one of the best known. It is the helmeted cassowary of science (*C. galeatus*). The third family, Dromornithidæ, is represented by the extinct Australian genus *Dromornis* (*Cat. Foss. Birds Br. Mus.* p. 355). The fourth suborder of the present super-suborder, or the Dinornithes, has been created to contain the family Dinornithidæ, a group susceptible of being divided into at least three subfamilies, and a number of genera (see *Trans. Zool. Soc.*, London, Vol. XIII, Part XI, October, 1895, p. 417). All these ostrich forms now appear to be extinct, although this extinction has taken place only within comparatively recent time. They were the moas of the islands of New Zealand, and were exterminated through the agency of the inhabitants of the islands. The fifth suborder of this group is represented by some five species of extinct ostrich forms of the island of Madagascar, all referred to the genus *Æpyornis*. This suborder has therefore been termed the *Æpyornithes*, and it has but the one family, *Æpyornithidæ*.

In Alfred Newton's *A Dictionary of Birds* under the article "Roc" will be found an excellent article giving the history of the discovery of these ancient ostriches, and excellent references to the literature of the subject. In the same work are found many other useful descriptions, the key to each of them occurring under the title "Ratitæ." Professor Newton there says: "According to the views adopted in this volume the subclass Ratitæ comprehends of existing forms the orders Apteryges (kiwi), Megistanes (cassowary, emeu), Rheæ (rhea), and Struthionες (ostrich), together with the extinct *Æpyornithes* (roc) and Immanes (moa). As regards the relation of other older forms to the Ratitæ [as Odontornithes and Stereornithes] it seems best at present to use reserve."

It is safe to say that all of the *typical* ostrich forms are descended from some common stock. As will be seen further on, the Apterygidæ are not considered to have any special relationship with the ostriches; they are altogether a different kind of bird.

A complete account of the comparative osteology of the Dromæognathæ would of itself make a large volume, so only such information as is necessary for the purposes of classification and to exhibit the general features of the skeleton among these birds is presented here.

Several years since I wrote out a brief account of *Struthio camelus*, with the intention of setting forth the various views entertained by avian taxonomers and osteologists as to its systematic position since 1865, and to give the main features of its skeleton. A good deal that I recorded was selected from the observations of Huxley, the Parkers, and others, for many anatomists have described more or less completely the osteology of *Struthio*, and have held many opinions as to its affinities. These opinions are becoming, however, more and more unanimous. The researches of the ornithopalæontologists have also greatly assisted the solution of the problem.

In my account referred to above I pointed out further that, of all the class Aves, *Struthio camelus* Linn. is the largest species of bird in existence, and it has been known, described, and written about for ages. Of recent years some naturalists have been disposed to recognize more than one form of African ostrich, but the claim has not as yet been fully established.¹

Suborder I. Struthiornithes.

Family STRUTHIONIDÆ: *Struthio camelus*.

Newton holds the opinion that "The genus *Struthio* forms the type of one group of the subclass Ratitæ, which differs so widely from the rest in points that have been concisely set forth by Professor Huxley (*Proc. Zoöl. Soc.*, 1867, p. 419) as to justify us in regarding it as an order, to which the name

¹ Newton, A. Art. "Ostrich," *Dictionary of Birds*, Pt. iii, pp. 662-666. The alleged differences seem to be purely of a superficial character.

Struthiones may be applied ; but that term, as well as Struthionidæ, has been often used in a more general sense by systematists even to signify the whole Ratitæ.¹ The most obvious distinctive character presented by the ostrich is the presence of two toes only, the third and fourth, on each foot, — a character absolutely peculiar to the genus Struthio.²

Huxley (*Proc. Zool. Soc.*, 1867) placed the genus Struthio alone in his first group, in the order (II) Ratitæ, while Garrod included all the ostrich-birds, tinamous, screamers, fowls, bustards, flamingoes, Musophagidæ, and Cuculidæ, in his order (I) Galliformes. Scater arranges them thus :

Subclass II, Ratitæ.
Order XXIV, Apteryges.
XXV, Casuarii.
XXIV, Struthiones.

Reichenow's scheme places them in a

Series I,
Order I, Brevipennes,
Family I, Struthionidæ,

including the entire assemblage of the once-called struthious birds.

In a Subclass IV (Eurhipiduræ), Stejneger classifies them thus :

Superorder I, Dromæognathæ.
Order I, Struthiones.
Superfamily I, Struthioideæ.
II, Rheoideæ.
III, Casuaroideæ.
Family I, Dromaiidæ.
II, Casuariidæ.
Superfamily IV, Dinornithoideæ,

followed by the remainder of his classification.

¹ At one time it was not uncommon to include the bustards among the Struthionidæ !

² Remains of a true ostrich have been recognized from the Sivalik formation in India, and the petrified egg of an apparently allied form, Struthiolithus, has been found in the south of Russia. Among the more important treatises on this bird may be mentioned: E. D'Alton, *Die Skelete der Straussartigen Vögel abgebildet und beschrieben*, folio, Bonn, 1827 ; Professor Mivart, "On the Axial Skeleton of the Ostrich" (*Proc. Zool. Soc.*, vol. viii, p. 385) ; M. Alix, *Essai sur l'appareil*

Fürbringer, in an order Struthiornithes, creates a suborder Struthioniformes, which is further subdivided into a "gens," Struthiones, and the family Struthionidæ. The Struthioniformes is an "order" in Dr. Sharpe's systematic arrangement of the class, an arrangement he clearly sets forth in his *Hand-List of Birds* (Vol. I, pp. 1-8, London, 1899). And thus we might proceed, giving one classificatory scheme after another, each and all practically presenting the same idea as to the position of the ostrich in the system. Reichenow's scheme, however, is a little antiquated now, while I hardly think that all naturalists will agree with Garrod in placing the cuckoos and flamingoes in the same "cohort," and these in the same order with the ostriches.

Huxley has said (*Proc. Zool. Soc.*, 1867, p. 419) the Afro-Arabian genus *Struthio* is the type of one group of this order (Ratitæ) characterized by:

1. The prolongation of the maxillary processes of the palatine bones forwards, beneath the maxillo-palatines, as in most birds.
2. The thickening of the inner edges of the maxillo-palatines, and their articulation with the facets upon the sides of the vomer.
3. The shortness of the vomer, which does not articulate with either palatines or pterygoids posteriorly.
4. The slight, or wanting, ossification of the prefrontal processes of the primoidal cranium.
5. The union of the bodies of the sacral vertebræ with the anterior ends of the pubes and ischia.
6. The presence of two shallow notches on each side in the posterior margin of the sternum.
7. The proportions of the fore limb. The humerus is about equal in length to the distance between the pectoral arch and the ilium, and is therefore much longer than the scapula. The antebrachium is not half as long as the humerus. The manus possesses the ordinary three digits; and two of these, the radial and the middle, are provided with claws.
8. The union of the pubes in a symphysis.

locomoteur des oiseaux (Paris, 1874); and Professor Macalister, "On the Anatomy of the Ostrich" (*Proc. Roy. Irish Acad.*, vol. ix, pp. 1-24).

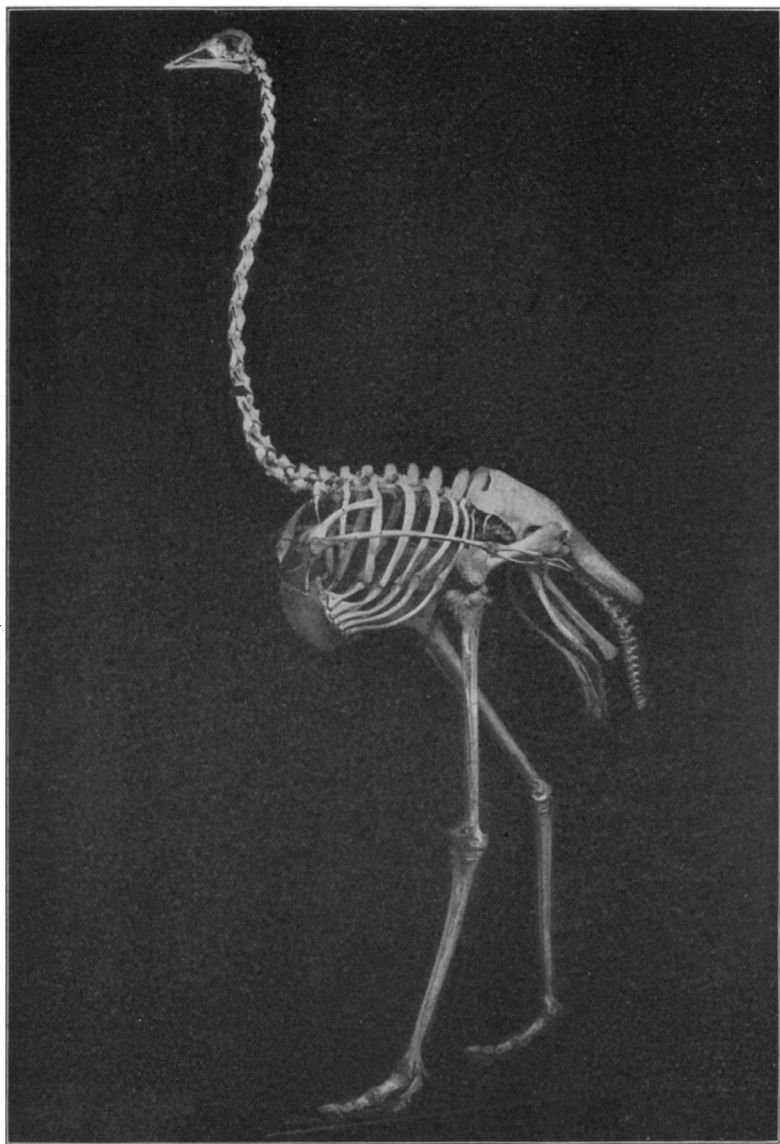


FIG. 1. — Skeleton of ostrich (*Struthio camelus* Linn.). Subadult, much reduced.
No. 13,806, Coll. U. S. Nat. Mus.

9. The abortion not only of the hallux, but also of the distal end of the metatarsal bone and of the phalanges of the second digit of the foot, whence the foot is two-toed.

10. The presence of thirty-five precaudal vertebræ.

In the same place Huxley gives the following osteological characters for the Ratitæ, or the "struthious birds," which "differ from all others in the combination" of these peculiarities (p. 418).

1. The sternum is devoid of a crest, and ossifies only from lateral and paired centers.

2. The long axes of the adjacent parts of the scapula and coracoid are parallel or identical. The scapula has no acromial process, nor has the coracoid any clavicular process; at most there are inconspicuous tubercles representing these processes.

3. The posterior ends of the palatines and the anterior ends of the pterygoids are very imperfectly, or not at all, articulated with the basisphenoidal rostrum, being usually separated from it and supported by the broad, cleft, hinder end of the vomer.

4. Strong "basipterygoid" processes, arising from the body of the basisphenoid and not from the rostrum, articulate with facets which are situated nearer the posterior than the anterior ends of the inner edges of the pterygoid bones.

5. The upper, or proximal, articular head of the quadrate bone is not divided into two distinct facets.

In his *Anatomy of Vertebrated Animals* Huxley has likewise pointed out that the cervical vertebræ in the Ratitæ have short transverse processes and ribs, disposed very much as in the Crocodilia, and I find that the ultimate vertebra of this series in the ostrich bears a pair of free cervical ribs (see Fig. 1). There appear to be nineteen of these cervical vertebræ, and six free dorsals, the latter developing lofty neural spines that gradually increase in height from before backwards. Fourteen or fifteen free caudals are also found in the chain, and these terminate with a stumpy pygostyle.

The dorsal ribs and their hæmapophyses are strong and substantial; the later exhibit a peculiar curving, and the epipleural appendages of the former are aborted in subadult individuals. Two pairs of short pelvic ribs are seen.

Sir Richard Owen, who published a great deal about the osteology of ostriches and their kin, both living and extinct, says of the sternum of *Struthio camelus* that "it is broader in proportion to its length, and subquadrate in the ostrich," and that in "all these keel-less sternums ossification begins, as in the ostrich, by a pair of centers expanding until they meet and coalesce in the middle line, and thence, according to the stimulus of the growth and pressure of the pectoral muscles, extending, as a keel, into the interspace."¹

In the pelvis of *Struthio* the ilia are long and narrow, their postacetabular portion being thoroughly and widely separated from the ischium upon either side (Fig. 1.), while in front the preacetabular region is shorter and much concaved externally. Huxley says: "In *Struthio*, alone, among birds, do the pubes unite in a median ventral symphysis. Another, not less remarkable circumstance, in the ostrich, is, that the 31st to the 35th vertebræ inclusively (counting from the atlas) develop five lateral tuberosities. The three middle tuberosities are large, and abut against the pubis and the ischium. In these vertebræ, as in the dorsal vertebræ of *Chelonia*, the neural arch of each vertebra shifts forward, so that half its base articulates with the centrum of the next vertebra in front; and the tuberosities in question are outgrowths, partly of the neural arch, partly of the juxtaposed vertebral centra, between which it is wedged. Hence, in young ostriches, the face of each tuberosity exhibits a triradiate suture."²

A conspicuous propubis is developed in the case of *Struthio*, and this has been figured by Owen (*Anat. Vert.*, Vol. II, p. 36, *m*), but in that figure the peculiar structure to which attention was invited by Garrod is not shown; this consists of a small osseous plate attached to the pubis, that is partly surrounded by cartilage.³ Forbes speaks of "this paper, written in conjunction with Mr. Frank Darwin," and points this out as the principal point of interest, and refers to it as "a peculiar nodule of bone lying on the center of the pubis and, in some respects,

¹ *Anat. Verts.* vol. ii, pp. 24, 25.

² *Ibid.*, pp. 251, 252.

³ Garrod, A. H. *Coll. Sci. Papers*, p. 99.

similar to the 'marsupial' bone of the implacental Mammalia and its corresponding fibrous representative in certain Carnivora."¹ As it has not yet received any special name it might be called the *suprapubic ossicle*. In Garrod's figure, where it is given, the pubis and ischium are firmly united posteriorly, as is also the case in Owen's figure, cited above, while in the pelvis of the ostrich in the collection of the United States National Museum these bones are distinctly independent of each other posteriorly (Fig. 1). Perhaps these do not unite until the bird is greatly advanced in age, and that this specimen is in a subadult stage of growth, which is the more likely as the epiphyses of the proximal extremities of the tarsometatarsals have not as yet coössified with the shaft.

Owen says in "the ostrich the two clavicles are distinct from each other, but are severally anchylosed with the coracoid and scapula, so as to form with them one bone on either side."

In the pectoral extremity the humerus of the arm is reduced to a mere curved and slender rod of bone, with slightly enlarged ends; while the radius and ulna of the antebrachium are even more decidedly aborted.

In *The Ibis* and in *The Philosophical Transactions of the Royal Society of London* (1888) W. K. Parker has given instructive figures of the manus of *Struthio camelus*, and they go to show that in the adult individual the radiale and ulnare ossicles of the carpus are separate and in bone. The phalanges have a most reptilian look, and the terminal joints of all three fingers are distally armed with a free, movable claw.

The pelvic extremity of *Struthio* is powerfully developed, all the bones present being massive and strong. Both the proximal end of the femur and its distal condyles are greatly enlarged. A patella is not developed in bone. The tibio-tarsus and tarsometatarsus are straight, and of nearly the same length. The distal end of the latter is modified for the articulation of the third and fourth digits, the only two toes possessed by this bird.

The cnemial process of the tibia is ossified by a separate epiphysis, in common with *Rhea*. Owen says the pneumatic

¹ Forbes, W. A. *Coll. Sci. Papers*, p. 203.

foramen of the femur in the ostrich is situated posteriorly rather than in front, as it is in nearly all other birds, while the "epicnemial process" of the tibiotarsus "extends forward, without rising above the level of the proximal surface, and contracting to its termination, there divides into small pro- and ecto-cnemial processes; the latter the shortest and tuberosus."

As for pneumaticity, the bones of an ostrich enjoy a greater degree of it than do those in the case of any of the true *Laridæ*.

Struthio camelus is, with respect to existing birds, most nearly related to the South American ostriches, the various species of *Rhea*.

The late T. J. Parker, in his admirable memoir "On the Cranial Osteology, Classification, and Phylogeny of the *Dinornithidæ*" (*Trans. Zööl. Soc., London*, Vol. XIII, Part XI, October, 1895), gives very complete tabular schemes comparing the cranial characters of several of the supersuborders of the *Dromæognathæ*, and from these it will be seen that a number of excellent characters distinguish the cranium of *Struthio* from that of *Rhea*.

Suborder II. Rheornithes.

Family: RHEIDÆ.

In the genus *Rhea*, the only genus of the present family, are contained those ostrich-like birds of South America, commonly known in Europe as nandu. According to Newton there are at least three species of these, *vis.*, *R. americana*, *R. darwini*, and *R. macrorhyncha*. Considerable has been written upon their osteology, but more particularly has the skeleton of *Rhea americana* been described, which received the attention of Huxley, of the Parkers, and of not a few others. Nearly all recent authoritative taxonomers place these birds in an order, coequal with the order occupied by the ostriches proper (*Struthio*).

Some of the special osteological characters of *Rhea* have been pointed out by Huxley, thus:

1. The maxillary processes of the palatines are short and unite with the inner and posterior edges of the maxillo-palatines.

2. The maxillo-palatines are thin, fenestrated plates, which do not articulate with facets on the edges of the vomer.

3. The vomer is as long as it usually is in birds, and articulates behind with the palatine and pterygoid bones.

4. The prefrontal processes are little ossified.

5. The bodies of the proper sacral vertebræ do not unite with the pubes or ischia ; and the centra of the sacral vertebræ, which ossify late, are extremely elongated and slender.

6. The short sternum narrows posteriorly and presents a notch in the middle of its posterior edge.

7. The length of the humerus exceeds the distance between the shoulder girdle and the ilium, and is of course greatly longer than the scapula. The manus has the same conformation as that of *Struthio*.

8. The pubes are free, but the ischia unite beneath the urosacral vertebræ.

9. The hallux is absent, but the second, third, and fourth digits are complete.

10. There are only thirty-two precaudal vertebræ. (*Proc. Zool. Soc.*, 1867, pp. 420-422.)

As in the case of *Struthio*, the skeletology of *Rhea* has long been known, and Prof. Kitchen Parker has, in his famous paper "On the Osteology of Gallinaceous Birds and Tinamous," given us a few of the necessary characters for the use of the taxonomer, they being presented in connection with what is there done with *Tinamus*.

The late T. J. Parker compared the skulls of *Struthio* and *Rhea* in his memoir on the *Dinornithidæ* (see *antea*), and showed that the differences existing between these two birds, in so far as that part of the skeleton is concerned, was in his estimation of ordinal rank. These distinctions, however, in the present work are considered to be but of subordinal value.

Suborder III. *Casuariornithes*.

Families : *DROMAIDÆ* (the emeus) ; *CASUARIIDÆ* (the cassowaries) ;
DROMORNITHIDÆ (extinct).

Huxley has already pointed out (*Proc. Zool. Soc.*, 1867, pp. 422, 423) that the osteology of *Casuarus* and *Dromæus* (emeu)

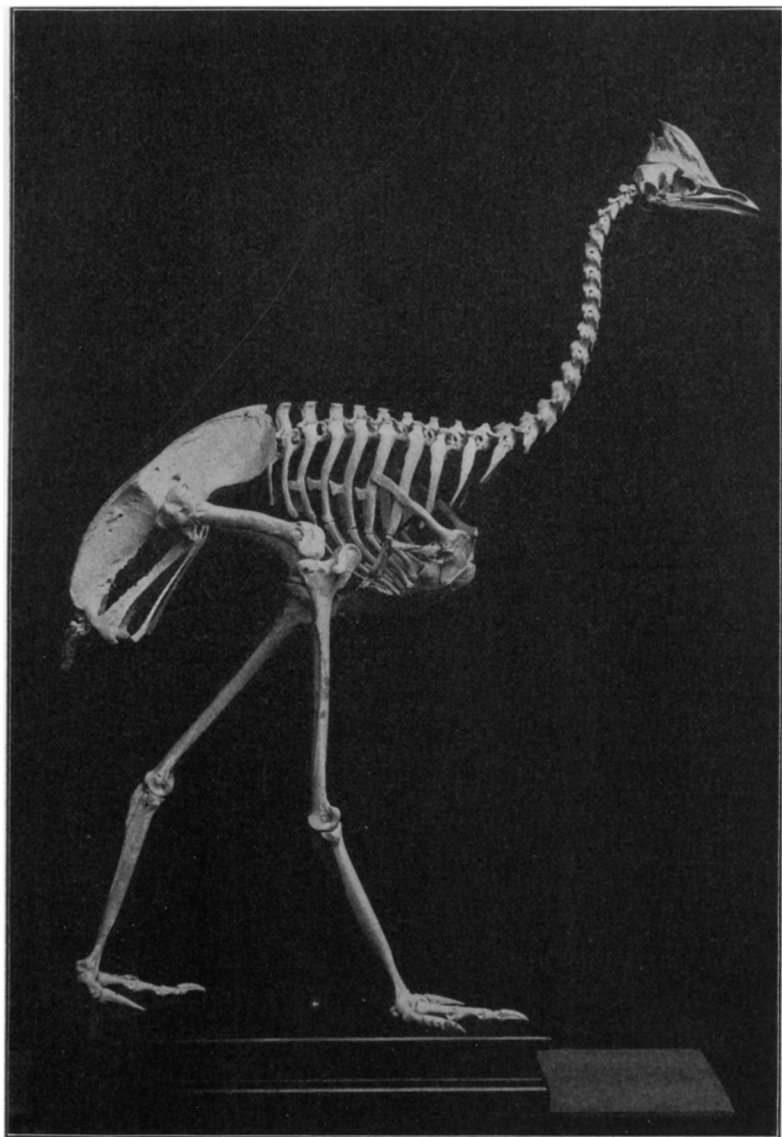


FIG. 2. — Right lateral view of the skeleton of *Casuarinus galeatus*, greatly reduced.
No. 16,964, Coll. U. S. Nat. Mus.

is much alike, and as a rule these birds have been by taxonomers properly considered to be more closely related than are *Struthio* and *Rhea* to each other. In the memoir just referred to, this eminent authority grouped the Malayo-Australian genera *Casuarius* and *Dromæus* together, and for this group gave the following osteological definitions :

1. The maxillary processes of the palatines are short as in *Rhea*.
2. The maxillo-palatines are flat, imperforate plates, which unite solidly with the premaxillæ and the vomer.
3. The vomer is long, and articulates behind with the palatine and pterygoid bones.
4. The prefrontal processes are large and well ossified.
5. The bodies of the proper sacral vertebræ do not unite with the pubes or ischia; and the bodies of the urosacral vertebræ are very large, thick, and well ossified.
6. The sternum is long and escutcheon-shaped, at first widening and then coming to a point behind.
7. The humerus is not nearly half so long as the distance between the pectoral arch and the ilium, and is much shorter than the scapula. The antebrachium is not more than half as long as the humerus. Only one digit, the median, is complete and bears a claw.
8. Neither the pubes nor the ischia unite in the middle line of the body.
9. The hallux is absent, but the other digits are complete.
10. There are thirty-five precaudal vertebræ.

Other osteological characters to be noted in the skeleton of *Casuarius galeatus* may be thus tabulated (see Fig. 2) :

1. The light, spongy osseous core surmounting the top of the skull. In life this supports the horny helmet.
2. There are nineteen cervical vertebræ, the last three bearing big free ribs that are without epipleural processes. There are *six* dorsals, the first five of which have ribs connecting with the sternum by means of hæmapophyses. Only the four in the middle of the series possess epipleural appendages; the last pair of ribs fail to connect with the sternum, as is also the case with the smaller pair of pelvic ribs present.

3. The external nostril is near the apex of the bill (Owen).
4. The clavicle is ankylosed with, or rather is a continuous ossification from the scapula; but the coracoid bone is free (Owen).

5. "In the adult Indian cassowary (*Casuarus galeatus*) there is only one carpal bone free; the manus is a solid single piece, with only one finger (the second, or index) developed, and this has only *two* phalanges — it ought to have *three*; and the distal phalanx is an inch long and carries a large claw" (Parker).¹

6. The *pelvis* resembles the pelvis in the emeu in form and in its main characters; but in *Dromæus* the ischium is, posteriorly, well separated from the ilium, while in the cassowary it fuses with it in that locality.²

7. The pelvic limb is powerfully developed: there is a big femur presenting many of the common ornithic characters, while the other bones of this extremity are also large, save hallux and first metatarsal, which are absent.

8. In the tibiotarsus the cnemial projections are conspicuously produced and rise to some extent above the proximal surface of the bone. The fibula has a massive head, while below its articulation with the shaft of the tibia it is tapering, slender, long, and styliform, ending in a free distal extremity.

9. The hypotarsus of the tarsometatarsus is a long, low median crest, and the unguis phalanx of the inner toe is especially elongated, straight, gradually tapering and distally pointed. The osseous claws of the other two toes are moderately curved, and exhibit proportions more in keeping with the remaining joints of their respective digits.

In T. J. Parker's memoir on the Dinornithidæ there is a tabular synopsis of the chief cranial characters of *Dromæus* and

¹ "In the ripe embryo of a specimen of the Mooruk (*C. bennetti*) I find *four* cartilaginous carpal nuclei and three metacarpal rays: the first is very small and feeble; the second very strong and with the normal number of phalanges (*i.e.*, *three* besides the metacarpal), and the distal or unguis joint is very long and carries a long claw; the third metacarpal is about one-sixth the size of the second, and has no phalanges on it. In the emu (*Dromæus*) the second digit has two phalanges and a long curved claw." *Ibid.*, W. K. P.

² Compare the side view of the pelvis in the plate with Marsh's figure of the pelvis of the emeu (*Ornithomimus*, p. 7, Fig. 16).

Casuarius recorded in a comparative way that is extremely useful (*Trans. Zool. Soc., London*, Vol. XIII, Part XI, October, 1895, pp. 410, 411). In closing the brief account of this suborder, especial attention is invited to the fact that the distal extremities of the ilium and ischium upon either side in the pelvis of Casuarius are firmly fused together as they are in all adult birds of the order Ornithuræ, and not free as in all ostriches known to us, either existing or extinct. Although very unostrich-like, yet no one with a knowledge of birds will ever question the claim of the cassowary to a place among the existing representatives of that group.

The representatives of the family Dromornithidæ are all extinct forms discovered in eastern (Dromornis) and southern (Genyornis) Australia. They here constitute the third family of the suborder Casuariornithes, but from the fact that they are fossil forms not far removed from the existing ostrich types, they will not be dwelt upon in this article. T. J. Parker has paid no little attention to them in his exhaustive memoir cited above. (See also Lydekker, *Cat. Foss. B.*, p. 355, 1891.)

Suborder IV. Dinornithes.

Family : DINORNITHIDÆ (the moas).

Considerable literature is extant of the extinct moas of the North and South islands of New Zealand. This is amply referred to in an admirable article, "Moa," by Lydekker, contributed to *A Dictionary of Birds*, by Newton. There one will find a number of moa's bones accurately reduced and figured with the remarks that "Moas are distinguished from all existing Ratitæ in having a bony bridge on the anterior surface of the lower end of the tibia above the condyles. The tarsometatarsus has three distal trochleæ, and in most cases (according to Capt. Hutton probably all) carried a hallux. The beak (unlike that of the kiwis) is short and stout; the form of the lower jaw being either U-like or V-like. The general form of the pelvis is very like that of the kiwis; but the sternum differs by the absence of the superior notch, the more divergent lateral processes, and the abortion or disappearance of the grooves for the coracoids" (p. 578).

The late T. J. Parker, who makes three subfamilies and five genera of the family Dinornithidæ (*Trans. Zool. Soc., London*, October, 1895, pp. 417 *et seq.*), has, among other extensive osteological comparisons of these birds, pointed out the following facts, which he tabulates thus :

The Skull in the Dinornithidæ.—Occipital plane vertical or very slightly inclined backwards or forwards ; occipital condyle pedunculate ; occipital crest variable. Length of cranial roof from two to two and a half times length of basis cranii.

Mammillar tuberosities usually prominent ; basitemporal platform always well defined and separated from occipital condyle by a deep precondylar fossa.

Width at paroccipital processes from less than one and a half to more than twice length of basis cranii.

Width at squamosals from about one and three-quarters to one and a half times length of basis cranii.

Height of cranium about one and a quarter times length of basis cranii.

Temporal fossa extends mesiad, to a greater or less extent, on to parietal region ; distance between temporal ridges varies from about width of cranium at temporal fossæ to half that width. Zygomatic process short, pointed, and nearly parallel to median plane ; auditory region of skull produced into a strong squamosal prominence.

Width of orbit about half width of cranium at paroccipital processes, and almost invariably less than length of basis cranii ; interorbital septum absent or greatly reduced ; a broad supraorbital ledge, produced behind into a strong, broad, post-orbital process.

Lacrymal ankylosed with frontal, forming preorbital process ; no orbital process ; a descending process ankylosed with outer border of antorbital, and notched or perforated for lacrymal duct. Mesethmoid produced into paired horizontal triangular processes. Antorbital well ossified ; ankylosed to descending process of lacrymal ; perforated dorsally by a supraorbital fenestra of variable size.

Nasal either has a slender maxillary process, or there is a distinct maxillo-nasal bone ; meets its fellow of the opposite

side in the middle line above the ethmoid, so that the latter does not appear on the dorsal surface; premaxillary groove on upper surface of nasals extends backwards to or beyond naso-frontal suture. Premaxilla strong; body more or less elevated, and with a distinct prenasal septum; palatine processes broad and produced into more or less definite vomerine processes; width of body always more than half and sometimes one and a half times length of basis cranii. Maxilla short and narrow; maxillo-palatine a short, flat plate, produced dorsad either into an irregular shell of bone containing a large antrum, or into a thick, oblique plate containing no, or but little, trace of the antrum.

Vomer less than one and a half times length of basis cranii; consists of thin paired plates meeting each other ventrad in an acute dihedral angle, and either quite free or partially ankylosed with one another in front; firmly ankylosed behind, in fully adult specimens, with palatines and pterygoids.

Palatine a thin twisted plate, about one and a fifth times length of basis cranii; pedate posterior end produced into short mesial vomerine process; articulates at anterior end with maxilla, and posteriorly with vomer and pterygoid, with which, in fully adult specimens, it becomes ankylosed.

Mandible very strong; symphysis short, more or less flattened and ridged below; distal end more or less deflected downwards.

The best part, or an extremely useful feature in connection with Parker's work, from which the above is quoted, is the excellent series of plates that illustrate it. These are devoted to the skulls of the various genera of the Dinornithidæ (Emeus, Anomalopteryx, Mesopteryx, Pachyornis, Dinornis), as well as a number of colored figures, showing the relationships to each other of the cranial bones in Emeus and Anomalopteryx.

Suborder V. *Æpyornithes*.

Family: *ÆPYORNITHIDÆ* (*Æpyornis*, the roc).

This group has been created to contain the now extinct ostrich-like birds of the island of Madagascar. Fossil and subfossil specimens of eggs and bones were first accurately

described and named by Isidore Geoffroy-St. Hilaire in 1851, who named this new ally of the ostrich *Æpyornis maximus*. This was confirmed later by M. M. Alphonse Milne-Edwards and Grandidier (*Ann. Sci. Nat.*, Ser. 5, Vol. XII, pp. 167-196, Pls. VI-XVI), and now the opinion is quite universally entertained among ornithotomists that these birds were ostriches related to the genus *Struthio* of the African continent or the adjacent mainland. It has been shown, however, that the largest species of *Æpyornis* thus far discovered, as indicated by its fossil remains, was by no means as big or as tall a bird as the larger species of the *Dinornithidæ* of New Zealand.

The fossil remains in the hands of science of these Madagascan ostriches are by no means abundant, consisting principally of bones of the trunk skeleton and of the lower extremity. Max Fürbringer¹ has discussed the value of these very fully as well as the work upon them by Edwards and Grandidier. It is not considered necessary in this brief article to redescribe these fragmentary remains, and there can be no question but what the birds they represent were a group of ostriches quite as distinct as the present existing ostriches of Africa (*Struthio*).

This concludes my brief survey of the osteological characters of the fossil and existing forms of the true ostrich birds. Before concluding the present article, however, I should like to call attention to a well-known fact, that it is very generally believed that *Apteryx* is closely allied to the *Dromæognathæ*, and should be grouped with them. Many claim that the family *Apterygidæ*, to which it belongs, is in the same suborder with the *Dinornithidæ*, but the more attention I pay to the phylogeny of birds the less and less do I see the glaring evidences of the struthionine affinities of these birds.

It would seem that other naturalists besides myself have, or do, entertain similar doubts upon this point. Dr. Sharpe in his admirable work *A Review of Recent Attempts to classify Birds*, in giving his ideal plan of an arrangement of birds in a museum in order to exhibit their relationships, says on page 59,

¹ *Untersuchungen zur Morphologie und Systematik der Vögel*. II, Allgemeiner Theil, pp. 1463-1465.

after he has grouped the ostriches together: "A little further afield we should come to the Apteryges, and here attention should be drawn to the ralline tendencies of these abnormal Ratitæ, with all those other peculiar characteristics on which it is not necessary here to dilate at length." Just why the Apteryx should be called "abnormal" more than any other bird living, or extinct, I fail to see. Any puzzling form may seem abnormal when persistent attempts are made to force it into an assemblage of other forms where it does not strictly belong.

Again, Fürbringer in his vertical aspect of the phylogenetic tree of birds has the branch Apterygiformes arise from the main trunk near the rails and far removed from any of the ostriches. In his opinion this Apterygian branch soon forked, however, and gave rise to the two families, Apterygidæ and Dinornithidæ. In his lineal scheme the position given these is in an order Alectoronithes, containing the Apteryges, the Crypturi, the Gallinæ, and the Opisthocomidæ. Many large groups both of land and water birds in this lineal scheme separate them from the ostrich birds, and it is very evident from all this that Fürbringer was of the opinion that the moas and kiwis are but very remotely related to the ostriches, the rheas, the emeus, the cassowaries, or any of the rest of that assemblage.

T. J. Parker commented upon this in the following words:

"The most definite opinion I have met with as to the phylogeny of the Ratitæ is that expressed in the elaborate genealogical tree which illustrates Fürbringer's great work. He ascribes a common origin to the moas and kiwis and to the emeus and cassowaries, but derives his four main groups of Ratitæ — the Struthioniformes, Rheiformes, Casuariformes, and Apterygiformes — separately from a primitive stock.

"Mivart, in his memoir on the axial skeleton of the Ratitæ (*Trans. Zoöl. Soc.*, Vol. X, 1871), gives no definite opinion as to the phylogeny of the group, but his diagram illustrating the mutual relationships of the various genera seems to indicate his belief in their monophyletic origin. He shows a main stem dividing into two branches; one of these divides again

for *Struthio* and *Rhea*; the other forks a second time, one branch dividing again for *Casuarius* and *Dromæus*, the other for *Dinornis* and *Apteryx*.

"The monophyletic origin of the *Ratitæ* is also supported by Newton, who, in his luminous article, 'Ornithology,' says 'that these forms — moa, kiwi, *emu* and cassowary, rhea, and finally ostrich — must have had a common ancestor nearer to them than is the ancestor of any carinate form' seems to need no proof.

"Professor Newton's classification indicates no closer affinity between any of the genera except the emu and cassowary, which together constitute his order *Megistanes*; each of the other genera has an order to itself.

"A study of the skull certainly confirms the view that the nearest ally of the *Dinornithidæ* is *Apteryx*, and that the four families of Australasian *Ratitæ* are more nearly related to one another than is either of them to the Asio-African and South-American forms. *Struthio* and *Rhea* differ so much from the Australasian members of the subclass as to lend strong support to Fürbringer's view that they arose separately from a primitive stock; but whether the cassowaries and emus on the one hand and the moas and kiwis on the other had a distinct or a common origin is a very complex question.

"The main difficulty lies in deciding what characters should be considered as of phylogenetic importance and what merely adaptive, but it appears to me that in the following particulars the emu and cassowary show an undoubted relationship to the moas.¹

"The general characters of the maxilla, maxillo-palatine, and antrum in both genera.

"The general relations of the vomer, palatines, and pterygoids in both genera.

"The presence of a vestige of the maxillary process of the nasal in *Dromæus*.

"The well-ossified antorbital ankylosed to the descending process of the lacrymal in both genera.

¹ "As my conclusions are based upon a study of the skull, I have omitted all reference to *Æpyornis*, *Dromornis*, *Megalapteryx*, and *Palæocasuarius*."

"The elevated body of the premaxilla with its distinct pre-narial septum in *Casuarus*.

"Forbes's discovery (*Trans. Nat. Zool. Inst.*, Vol. XXIV, 1891, p. 185) of a dinornithine bird which he calls *Palæocasuarinus* will, if the detailed account of his very interesting researches bears out the opinions expressed in his preliminary note, lend strong support to this view. The tibiae upon which the genus is founded have, as the name implies, a remarkable resemblance to those of the cassowary.

"On the other hand, I know of no character in the skull of *Rhea* by which it definitely approaches the moas, and the presence of a maxillary process to the nasal, the form of the cerebral fossæ, and the position of the pneumatic foramen of the quadrate seem the only particulars in which the ostrich comes in any way near them. *Struthio* and *Rhea* are, in fact, sharply separated both from one another and from the Australasian *Ratitæ*, as well by the characters of the bony palate as by those of the pelvis. The characters possessed by them in common with the other *Ratitæ* are of two kinds: ancestral characters, such as the form of the vomer, the basipterygoid processes, and the single-headed quadrate, which, according to the view taken in this paper, are accounted for by the hypothesis of common descent from a group of generalized flying birds or *Proto-Carinatæ*; and adaptive characters, such as those of the sternum, shoulder girdle, and wing, which they share to a greater or less degree with all flightless birds.

"The marked differences between the moas and kiwis are certainly for the most part adaptive; the two families resemble one another in the increased size of the olfactory organ and the reduced size of the eye; but both processes have gone so much further in *Apteryx* that the differences between the two, in this respect alone, give the skulls the appearance of being more widely separated than those of any other two ratite birds. The real affinities underlying these differences are, however, shown by the striking similarity of the bones of the palate in the two forms. The absence of a maxillary antrum in *Apteryx* seems at first sight a difference of great importance, but the fact that this cavity has disappeared or become vestigial in one of the

most specialized genera of the moas seems to indicate that its complete atrophy in the kiwi is simply to be looked upon as an instance of the extreme specialization of that genus."

I have thus fully quoted from T. J. Parker's views upon the relationships of the ostriches and Apteryx for the reason that they are important and useful in the present connection, and that they are entertained by many other naturalists. It must be remembered, however, that these views are drawn up after an examination of the bony skulls alone, or very nearly alone. It must be borne in mind, too, that Marsh endeavored to make ostriches, or ratite birds, out of Hesperornis and Ichthyornis simply because they possessed the ancient form of palate, and that their ilia and ischia possessed free posterior extremities.

I now pass to a consideration of the osteological characters of the Odontoholcæ, the supersuborder to which the Hesperornithidæ belong. It will be necessary to reproduce my observations in order to properly set forth and support my scheme of classification which, as I have already said, will be published in the future.

SUPERSUBORDER III. ODONTOHOLCÆ.

SUBORDER.	SUPERFAMILY.	FAMILIES.
Pygopoformes.	Hesperornithoidea.	Hesperornithidæ. Enaliornithidæ.

Fossil remains of upwards of fifty individuals representing extinct species of the Hesperornithidæ have been taken from the Middle Cretaceous of Kansas and Colorado, where occurred also Ichthyornis (Order II) and its allies. Marsh also described the bones of these great ancestral divers in his *Odontornithes*, and left us a restoration of the skeleton of *Hesperornis regalis*. This was not a difficult task for the reason that nearly perfect skeletons of that form were deposited in the museum of Yale College, and one of these was so complete that it lacked only a very few unimportant bones, as the distal ungual phalanges of two or three of the podal digits.

Hesperornis regalis had a length of about six feet, and an adult specimen when assuming the erect attitude would have had a height of about three feet. The distinguished Scotch

anatomist, D'Arcy W. Thompson, and myself have carefully examined into the osteology of these extinct divers, and have shown that they undoubtedly are among the ancestors of the existing Pygopodes (*vide postea*).

The skull of *Hesperornis* in its general formation resembles closely the skull of such a diver as *Urinator lumme*, but exhibits characters common to many birds belonging to widely separated groups of the age in which it lived. For example, the capacity of the cranial casket was small; the superior articular head of the quadrate bone had but one articular facet; they had teeth in grooves, all the length of either ramus in the lower jaw, but confined to the dentary borders of the maxillaries in the case of the upper. The ramal symphysis was cartilaginous throughout the life of the individual, and consequently each ramus was a separate bone.

According to Marsh, the proximal extremities of the palatines and the distal ends of the pterygoids did not articulate with the basisphenoidal rostrum. The stout basipterygoid processes arose from the body of the basisphenoid, and each one articulated with a facet upon the corresponding pterygoid situated near its proximal end. It had separate vomers. The supraorbital glandular depressions, the holorhinal nostrils, the firmly united intercranial sutures, the form of the quadratojugal, and many other characters, exhibiting but little change in their now living descendants, are each and all characteristic of the Pygopodes. As the teeth do not belong to the skeleton, they require no special description in an article devoted to osteology; be it sufficient to say that they were purely of a reptilian type.

The mandible was long and slender, and "the rami were united at the symphysis in front only by ligament, a feature unknown in modern adult birds. There is an imperfect articulation between the splenial and angular elements, which probably admitted of some motion, and all the other sutures are open, or distinguishable. There was apparently a mandibular foramen. There is a well-marked shallow groove on the outer superior margin of each dentary bone for the reception of the maxillary teeth when the jaws were closed. The angle of the mandible extends backward but a short distance beyond

the articular face for the quadrate, and the extremity is obliquely truncated" (Marsh). *Hesperornis regalis* possessed 49 vertebræ in its vertebral column, or 23 presacrals, 14 sacrals, and 12 caudals. Both in the articular facets of the centra and in other characters they agree with such modern genera as *Urinator* and other divers. In its caudal skeleton this great cretaceous diver was peculiar, the free anterior caudal vertebræ being short, with lofty neural arches and not conspicuous diapophyses, and exhibited an opisthocœlian articulation. Great horizontal expansion characterized the long transverse processes of the mid and posterior caudals, while the last three or four elements of this part of the vertebral chain coössified together in the adult, forming a *flat*, horizontally compressed, pygostylous mass, very different from anything to be found in the form of the terminal piece in the tail of existing Aves. None of the presacral vertebræ united, and none of the caudals possessed zygapophyses. It is very likely that *Hesperornis* used its broad, horizontally flattened tail much as the now-existing beaver among modern mammals employs its paddle-like caudal appendage, — a powerful aid as a propeller and rudder to the aquatic locomotion of this ancient pygopodous fowl.

The sternum in this genus is flat and broad and thin posteriorly. Anteriorly, it is rounded and projecting, while but two shallow notches are to be seen in its xiphoidal margin. The ribs, some of them bearing uncinate processes, resembled those of the loons, but the shoulder girdle, with its non-united clavicles, was weak and small in character, and the pectoral limb was reduced to a rudimentary humerus.

The pelvis of *Hesperornis* was like the pelvis of our modern loons and grebes, and Marsh observed that it resembles that of *Podiceps*, being very long and narrow, as in that genus, and in other diving birds. He also remarked that the "acetabulum differs from that in all known birds, in being closed internally by bone, except a foramen that perforates the inner wall, as in the crocodiles. The ilium, ischium, and pubis, moreover, have their posterior extremities free and distinct."

The powerful bony framework of the pelvic limbs of this great extinct diver agrees in many characters with the corresponding

parts in the skeleton of the legs in grebes and loons. This has also been noted by Stejneger, and Marsh said in his *Odontornithes* that the "posterior limbs of *Hesperornis regalis* present an admirable example of adaptive structure. The means of locomotion were confined entirely to these extremities, and the life of *Hesperornis* was probably more completely aquatic than that of any known bird. It may fairly be questioned whether it could even be said to walk on land, although some movement on shore was of course a necessity. Considering the posterior limb as a whole, it will be found a nearly perfect piece of machinery for propulsion through the water. Provision was made for a very powerful backward stroke, followed by a quick recovery, with little loss by resistance, a movement quite analogous to the stroke of an oar, feathered on its return.

"Among recent birds, we have, in the genus *Podiceps*, the nearest approach to the legs and feet of *Hesperornis*, and the osseous structure of these parts is essentially the same throughout in the two genera. The muscular system, also, of this member must have been very similar in both. In many respects, however, the bones of the posterior limbs of *Hesperornis* present evidences of a more primitive structure than is seen in any recent diving birds."

The femur was remarkably short and stout, being flattened in the antero-posterior direction. The large, rounded head was supported by a short, strong neck, and excavated above by a pit for the ligamentum teres. Trochanter major was large, and the entire proximal end of the bone possessed an articular surface for the antitrochanter. As in *Urinator*, the shaft was curved, and exhibited strong prominences for muscular insertion. Expanded distally, the outer condyle was the larger of the two, and only a shallow groove divided it from the inner one.

Tibiotarsus was a long, powerful bone, by all odds the biggest one in the skeleton of this bird. It much resembles the same bone of the leg in any of our typical grebes. At its distal end, as in *Podiceps*, there is no osseous bridge in front spanning the longitudinal muscular groove below.

A very large free patella was developed, and it was pierced by a foramen to transmit the tendon of the ambiens muscle, as

in *Sula*. Compressed transversely, it was distinctly triangular upon lateral aspect.

Marsh observed that the fibula of *H. regalis* agreed essentially with that of *Podiceps*, and, as in that genus, the entire skeleton of the limb is non-pneumatic. "In the adult *Hesperornis*, the second, third, and fourth metatarsals are thoroughly coössified into a stout, transversely compressed bone of moderate length, but in most specimens traces of the sutures remain. The fourth metatarsal element so greatly exceeds the other two in size, that it forms by far the greatest part of the entire tarsometatarsal bone.

"The first metatarsal is not coössified with the main shaft of the tarsometatarsal bone, but is a mere remnant, united to the lower half of the second by cartilage [ligament?]."

Different species of *Hesperornis*, as *H. crassipes*, *H. gracilis*, and *H. regalis*, exhibited marked characteristic differences in the various bones of their skeletons. But they were only of specific value.

Of the skeleton of the foot in *H. regalis*, Marsh wrote that the feet of "*Hesperornis* resembled more closely those of the genus *Podiceps* than of any other birds. The number of digits is the same, the number of phalanges in each digit identical, but the proportions of the latter are different and quite peculiar. In *Podiceps*, and the other grebes, the outer toe is the longest, but the middle one almost equals it in length and size, while the second is but slightly smaller. In *Hesperornis*, however, the fourth or outer toe is the dominant one, being three or four times as powerful as the adjoining one, or as the other three combined. Again, the phalanges in *Podiceps* are very elongated and slender, and the terminal ones spatulate, while, in *Hesperornis*, the phalanges are short and thick, with the terminal ones more or less pointed. The phalanges in *Hesperornis* are, in fact, shorter than in most swimming birds, and in their individual proportions remind one of the toe bones of the penguins" (*Odontornithes*, pp. 99 and 100).

Fossil remains of many other birds have been discovered in the cretaceous formation in different parts of America, and a number of these have been described and named by Marsh

and others, but the few bones thus far in the hands of science are too fragmentary to admit of saying to what manner of birds they belonged, much less as to the affinities of the several forms they represent. Others have also come to light in Europe to which the same remarks apply.

As I have already pointed out in the *Journal of Anatomy* (London, April, 1892, p. 202), I consider all the species of the genus *Hesperornis* as having belonged to a family *Hesperornithidæ*, and this family may possibly have been an offshoot of a superfamily, the *Hesperornithoidea*, which contained forms possessing the power of flight; and from these latter our present *Pygopodes* have descended, while the offshoot-genus *Hesperornis* died out during the cretaceous time, and left no direct descendants.

What I have said elsewhere in regard to the characters in the skeletons of these ancient birds not possessed by their representatives of the present age, applies also to *Hesperornis*. For example, the structure of the palate, the extremities of the pelvic bones being free, and so forth, are derived from their reptile ancestors just as the ostriches derived theirs, and the last named are now existing forms that have carried them down.

Family: ENALIORNITHIDÆ.

Of the remains of the fossil *Enaliornis* I know nothing beyond what I have learned from reading. Lydekker, in the article "Fossil Birds," in Newton's *Dictionary of Birds* (p. 280), has said, "In 1858 Barrett discovered in the Upper Greensand of Cambridgeshire remains described by Professor Seeley in 1866 (*Ann. and Mag. Nat. Hist.*, Ser. 3, Vol. XVIII, p. 100) under the preoccupied name *Pelagornis*, but in 1867 renamed *Enaliornis* ('Index to Aves and Reptilia, Camb. Mus.,' *Quart. Journ. Geol. Soc.*, Vol. XXXII, p. 509). These indicate a bird apparently allied to *Colymbus*, and not improbably to *Hesperornis*."

Fürbringer fully discusses what is known of the *Enaliornithidæ* (pp. 1152, 1153) and is satisfied of the relation of *Enaliornis* to the extinct toothed loon, *Hesperornis*, as well as to the various existing *Pygopodes*, and classifies it accordingly.